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Coming home: Back-introduced invasive genotypes might pose an underestimated risk in the species´ native range

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Abstract

Biological invasions are considered a significant challenge both from an ecological and economical perspective. Compared to the native range, environmental conditions in the invasive range often favor more competitive genotypes. Little attention, however, has so far been paid to the possibility that these invasive and competitive genotypes might also be back-introduced into a species' native range, where they could trigger a problematic increase in abundance or expansion. The frequency with which this occurs in the species´ native range might be an underestimated aspect in nature conservation. We transplanted native and invasive individuals of the biennial model species *Jacobaea vulgaris* into field sites of naturally occurring populations within the species' native range. The aim was to test whether back-introduced invasive origins show decreased performance, e.g., because of the reunion with specialized herbivores or plant-soil-feedbacks or whether they have the potential to trigger problematic population dynamics in the species' native range. We ran an additional greenhouse experiment to specifically address soil-borne effects in the species' native habitats. We found that invasive individuals generally outperformed the native transplants if compared in the field sites. By contrast, there were no origin-dependent differences in the greenhouse experiment. Our findings clearly indicate that testing for origin effects exclusively under controlled conditions might underestimate the potential of invasive genotypes to trigger invasion processes in habitats of the species' native range. Although differences in performance mediated by soil-borne effects were not associated with plant origin, field site susceptibility to *J. vulgaris* colonization varied largely. Identifying the exact factors driving these differences, offers another focal point to minimize the risk of a detrimental increase in the abundance or expansion of this highly invasive species in its home range.

Keywords

cryptic invasions, enemy release, local adaptation, plant-soil-feedback (PSF), ragwort, re-introduction, transplant experiment

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Introduction

Invasive alien plant species pose a significant threat to biodiversity (Gaertner et al. 2009; McGeoch et al. 2010; Vilà et al. 2011) and particularly for endangered native species (Pimentel et al. 2005). Given that invasive species might benefit from ongoing climate change (Liu et al. 2017) and increasing human activity (Sardain et al. 2019), the situation might even exacerbate in the future as attempts for predicting invasive species as well as vulnerable habitats have so far been proven to be difficult (de Andrade et al. 2019; Miller et al. 2020). This might particularly apply to "cryptic invasions", a special case of these biological invasions (Morais and Reichard 2018) often completely overlooked when addressing threats to biodiversity. Recognition of invasion processes might fail because invasive plant species are misidentified (i.e., interspecific cryptic invasion) or because the invasion is triggered by the addition of a non-native lineage/genotype (i.e., intraspecific cryptic invasion). Cryptic back introduction, whereby genetic material from an invasive population is translocated back to the species' native range, might pose a particularly high risk (Guo 2005). However, while interspecific cryptic invasions are increasingly being noticed (e.g. Alves et al. 2021; Goodman et al. 2021; Mezhzherin et al. 2022), intraspecific cryptic invasion might be the hidden cause of a sudden increase in abundance or rapid range expansion in a native species that is regularly attributed to changes in the environmental conditions instead (Morais and Reichard 2018). Subsequently, an observed range expansion of a native species might go undetected as a biological invasion.

Given the increasing human mobility around the globe that allows plant species to overcome the first barrier in the invasion process (Blackburn et al. 2011), as well as the intensified global floristic homogenization (Yang et al. 2021), it seems reasonable to assume that, once established, invasive populations might also be transported back to the species' native range. In fact, the lizard *Anolis sagrei* originating from Cayman Brac and Little Cayman, became invasive on Grand Caymen and was later back-introduced to Cayman Brac (Kolbe et al. 2017). In a similar vein, cultivars of *Ilex aquifolium* were found to promote the native range expansion of wild populations (Skou et al. 2012). Those cryptic invasions, similar to biological invasions by native-alien populations, might be underestimated in their impact (Nelufule et al. 2022). In a study regarding assisted migration, Mueller and Hellmann (2008) found that intracontinental invasions, though rare, are usually as detrimental as intercontinental invasions. Brandes et al. (2019) were able to suggest a cryptic intracontinental invasion to have taken place in the native range of scotch broom by alien genotypes. However, uncovering cryptic invasions, in particular, is difficult as conspicuous signs are usually absent.

In general, range expansions in any population, native or invasive, are associated with adaptations that facilitate high reproduction rates (Fronhofer and Altermatt 2015) and allow counteracting formerly limiting environmental factors (Colautti and Barrett 2013). In a novel range, populations may encounter biotic and abiotic conditions that differ from the species' native range (e.g. Mitchell et al. 2006) and that thus represent selective forces to adapt to. Introduced populations may ultimately exhibit

fundamental niche shifts, for example in regard to climatic conditions in a species' novel range (Broennimann et al. 2007; Early and Sax 2014). If these adapted novel genotypes are back-introduced to the species' native range they might show considerably different performance back in the species' native habitat than in the novel one.

For example, species naturalized outside their native range often experience a release from natural enemies during the invasion process. Once exempt from the necessity to defend against specialist herbivores occurring in the plant species' native range, resources can be used for other purposes (Enemy Release Hypothesis) (Keane 2002). In a broader understanding, differences in the biotic environment with its trophic interactions, i.e. pathogens, herbivores (specialists as well as generalists) and/or predators, are part of a possible enemy release. A release from those constraints may then be transformed into a stronger competitive force through resource redistribution (Erfmeier 2013). Consequently, selection then favors genotypes that invest less in now obsolete defenses and more into other traits supporting fitness. Ultimately, invasive genotypes are often subject to selection towards a higher competitive ability compared to their native counterparts (Evolution of Increased Competitive Ability hypothesis) (Blossey and Nötzold 1995; Broennimann et al. 2007). These processes can cause a noticeable increase in both the distribution and local abundance of invasive species. When those invasive genotypes are subsequently back-introduced, the loss of defenses against specialized herbivores and/or pathogenic soil biota could prove to be a maladaptation but could also facilitate subsequent changes in native populations. In the past, common garden experiments in a species' native range often found invasive populations to show inferior performance when compared to their native counterparts (Maron et al. 2004; Hock et al. 2019; Pal et al. 2020).

Besides the often-addressed aboveground factors, such as herbivory, plant-soil-feedbacks (PSFs) have gained more and more attention and call for a belowground focus. In recent years, PSFs are of increasing interest as part of the environmental factors contributing to the success or failure of the invasive range expansion process. While the aforementioned effects of enemy release mostly refer to aboveground herbivores, invasive populations might similarly be freed from enemies in the soils (Beckmann et al. 2016), lose beneficial mutualists (Zenni et al. 2017) or they can encounter new detrimental (pathogens) or beneficial (mutualists) interactions (Reinhart and Callaway 2006). For *Centaurea solstitialis*, e.g., the release from soil pathogens may have been a crucial factor determining its success as a highly invasive species (Montesinos and Callaway 2020). Furthermore, allelopathy exerted by naturalized alien plant species on native plant species was found to have a greater negative effect than allelochemicals from other co-evolved native plant species (Zhang et al. 2020). This indicates that belowground processes may certainly contribute to invasive population dynamics and range expansion.

Accordingly, both above- and belowground agents, such as aboveground herbivory and plant-soil feedbacks, should be considered jointly when trying to judge the success or failure of (exotic) populations. Yet, most studies usually have an either exclusively aboveground or belowground perspective. However, trophic interactions may affect

all plant organizational components. Furthermore, common gardens are typically not established as in-site experiments within naturally occurring populations of a species under consideration. This is understandable for reasons of nature conservation. However, abstaining from this kind of test means disregarding the role of PSFs. They can be exerted by the species itself or by co-occurring species and should be addressed in the complex context of the whole set of environmental factors. Consequently, conducting controlled experiments in-site is the best way to adequately assess the risk of both classical biological invasions and cryptic invasions.

The biennial model species *Jacobaea vulgaris* Gaertn. (ragwort), native to Eurasia, is a successful invader on at least two continents and several studies have already provided evidence for genotypic differentiation between native and invasive plant origins. Invasive *J. vulgaris* individuals were shown to grow larger both in a greenhouse (Joshi and Vrieling 2005) and in a common garden experiment (Stastny et al. 2005), thereby providing evidence for an evolutionary shift, that is at least partly connected to herbivore composition differences between the species' ranges. Another common garden experiment, however, found no differences in biomass between origins (Rapo et al. 2010). Here, the authors concluded that the absence of origin-dependent differences might be due to the high-competition setting of their experiment, thus further emphasizing the necessity to study the performance in real-life settings.

In the last two decades, *J. vulgaris* also exhibited a severe increase in abundance in Northern Germany as part of the species´ native range which made it a target species for management efforts in the species' native range as well (Möhler et al. 2021; Schwarz et al. 2021). Therefore, although invasive *J. vulgaris* genotypes might be expected to underperform in the species' native range, it is a good candidate to assess the risk for cryptic invasions through back-introduction that might counteract management efforts in the species' native range. Additionally, there is evidence for PSFs exerted by *J. vulgaris* affecting the performance of other species (Kos et al. 2015a, b) but also for PSF effects on the species itself (van de Voorde et al. 2011, 2012a). In particular, autotoxicity, as one agent transmitting PSFs in this species, has been proposed as a factor driving the decline in abundance in later successional stages (van de Voorde et al. 2012b; Möhler et al. 2018). Hence, when examining the invasive potential of *J. vulgaris*, common garden experiments including the entirety of environmental conditions should be carried out, i.e., ideally within natural populations that might exert those PSFs. Specifically, when aiming to elucidate the potential for cryptic invasions by back-introduction of invasive genotypes, experiments should be carried out within natural native populations to receive realistic outcomes of such a scenario.

We carried out a transplant experiment in field sites of naturally occurring ragwort populations in the species' native range. We aimed to test whether *J. vulgaris* individuals of invasive origins do, in fact, underperform in field sites in its native range. Alternatively, if they grow better than native plants, they thus have a potential to contribute to intraspecific cryptic invasions once back-introduced. To address how differences in observed performance might be related to environmental factors, we assessed soil abiotic information (soil moisture, CN and pH) just as biotic community information (*J. vulgaris* population density, species richness/α-diversity and vegetation height as proxy for productivity).

We additionally considered relative light availability, and bare soil proportion within every plot. This set-up allowed us to test (I) whether invasive genotypes show maladaptation to the species' native habitat. If maladaptation does not prove true, *J. vulgaris* would then be a potential candidate for problematic outcomes of back-introduction events. We also tested (II) what environmental factors might contribute to the observed patterns. Furthermore, in an additional greenhouse experiment using the same populations as in the field trial, we studied (III) the extent as to which, in particular, negative soil-mediated impacts display genetic divergence between origins, i.e., are more expressed in individuals originating from the invasive than from the native range.

Materials and methods

Study species

Jacobaea vulgaris Gaertn. (Asteraceae, formerly *Senecio jacobaea*) is a predominantly biennial herbaceous plant species regularly observed with annual or perennial life-cycles (Wardle 1987). Flowering in the second year is positively influenced by size of the first-year rosette (van der Meijden and van der Waals-Kooi 1979) and nutrient availability (Prins et al. 1990). Each flowering individual may produce up to 30,000 achenes (Harper and Wood 1957). *Jacobaea vulgaris* is native to Eurasia (Harper and Wood 1957). After several introductions to various places, *J. vulgaris* today, is considered invasive in North America (Isaacson 1973) and Australia (Schmidl 1972).

Seed collection and preparation

Seed collection was carried out in the summer of 2018 in the Pacific Northwest (invasive range) and Central Europe (native range) at the same time. For species identification, we referred to "Rothmaler - Exkursionsflora von Deutschland" (Jäger 2017) and local plant identification literature. We sampled 22 invasive and 24 native populations, spanning a maximum distance of 524 km and 742 km, respectively. For each population, achenes (hereinafter seeds) of 20 maternal plants were collected, if available. The seeds were stored separately by seed family (i.e., seeds from the same maternal plant) in paper bags at room temperature in the lab of the Institute for Ecosystem Research (Kiel University) until use.

Six populations each by range of origin (invasive – native) were chosen according to seed quality and availability to be included in this experiment. In addition, we intentionally included populations varying in size and density in order to cover a broad range of variation within ranges. The sites in the native range served both as donor populations for seed sourcing and target sites for (re-)transplantation. For the selection of these six native populations, we thus additionally had to acquire permission from local authorities, landowners, and the tenant farmers for conducting a transplant experiment on their sites. All field sites for this experiment are owned by the Stiftung Naturschutz Schleswig-Holstein (for population information, s. Suppl. material 1: fig. S1).

From each population, seeds from seven randomly selected seed families were sown in potting soil (TKS 2 pot Medium Coarse, Floragard Vertriebs-GmbH, Oldenburg, Germany) on germination trays in April of 2019. The seeds were covered by 1 cm of soil layer to prevent them from drying out. The germination trays were placed in a greenhouse cabinet with ambient temperature and a photoperiod of 12:12 (night/day) hours and watered daily in the following days. After four weeks, five seed families with the highest germination success within each population were chosen to be included in the experiment and seedlings were thinned to allow optimal growth. Once established, the germination trays were placed outside to allow acclimatization of the separated individuals to outdoor conditions.

Experimental set-up: Field experiment

The field experiment was designed to estimate performance of invasive individuals compared to native individuals in the species' original native range. The location of the six native populations used for seed material sampling also served as transplantation sites. In each of these six sites, we established five experimental plots. Plot locations were assigned randomly within site with coordinates marking the southwest corner of each plot. Starting from this corner, an area of 0.9 m × 1.2 m was established, where transplants were arranged in 4 × 5 rows (all plants were 0.3 m apart) leading to a total of 20 planting positions. One individual from each of the six invasive populations and two individuals from each of the six native populations (and therefore also originating from the experimental sites (= at their population home)) were randomly assigned to the planting positions leaving out the southwest and northwest spots. Thus, a total of 18 individuals were planted per plot. Each two individuals from the six native populations were replicates from the same seed family. For each of those replicates, one individual was a priori randomly chosen for the present experiment while the second one was assigned to remain into the summer of 2020 as part of an additional experiment (s. Suppl. material 1: fig. S2 for schematic overview). Therefore, 12 of the 18 individuals per plot (6 native and 6 invasive) originally belonged to the experiment described here. In case of mortality, however, the native replicate individual served as a substitute in the present experiment (except for the assessment of survival). All remaining individuals were removed before flowering in summer 2020 to ensure prevention of seed set and dispersal.

Planting was carried out starting June 15th 2019 (approx. 2 months after sowing). The vegetation in the plots was cut to approx. 0.3 m to reduce heterogeneity during early establishment of the experimental plants. Subsequently, experimental plants were brought out with the adhering potting soil and labelled for recognition. After planting, each experimental plot was watered with 10 l water right away and two additional times after one week to assure establishment and survival of the planted individuals.

Next to each of the five experimental plots, a 2 m × 2 m monitoring plot was established following the diagonal extension 5 m apart in a northeastern direction. The monitoring plots served for recording vegetation composition and structure, including information on overall vegetation height (as a measure for productivity), coverage using a modified Londo scale (Londo 1976) and percentage of bare soil. Soil samples

were taken next to the monitoring plot for soil C:N determination (with a EURO Elemental Analyzer) and determination of pH in the laboratory at the Institute for Ecosystem Research, Kiel University. In the monitoring plots, *Jacobaea* abundance (i.e., naturally occurring individuals) was additionally determined to infer local population density. Soil moisture was measured at the four corners of the experimental plot using Time Domain Reflectometry with ML3 Theta-soil moisture sensor (Delta-T devices Ltd, Cambridge, United Kingdom). Mean relative light intensity was determined from four evenly distributed measurements taken within each experimental plot (LI-1500 Light Sensor Logger, Li-COR Biosciences, Lincoln, United States).

The monitoring of the field experiment ran from June 28th until September 28th. After 6 weeks and 14 weeks of experimental runtime, we determined specific leaf area (SLA) and leaf dry matter content (LDMC) of transplants. For this, the third fully developed leaf from the top was taken from each plant and stored in a moisturized plastic bag in a cooler box for transportation to the lab. Fresh leaves were scanned (Expression 11000XL, EPSON Deutschland GmbH, Meerbusch, Germany) and leaf area was determined using WinFolia (WinFolia Pro 2015, Regent Instruments Inc., Quebec, Canada). Leaf fresh weight was determined using a precision scale (Sartorius 1702MP8, Sartorius AG, Göttingen, Germany). All leaves were dried at 65 °C for 48 hours afterwards for subsequent dry weight determination. At the end of the experimental runtime, we determined the transplants' expansion in two directions (to calculate rosette size), the number of healthy leaves, and length of the longest leaf. Herbivory was assessed as a binary trait and considered present when parts of the leaf were missing or by the appearance of characteristic "bullet-holes" caused by *Longitarsus jacobaeae*. For biomass determination, all invasive individuals and half of the native individuals were dug up (i.e. 12 individuals per plot). Dry weight was separately determined for aboveground and belowground biomass after drying in a drying oven at 65 °C for 48 hours. We additionally calculated the root:shoot ratio as a measure for resource distribution strategy.

Experimental set-up: Greenhouse experiment

The greenhouse experiment was set up analogous to the field experiment and ran from August 21st (approx. 4 months after sowing of seeds) to November 13th. To decouple the influence of soil biota effects from other environmental factors varying with the field sites, soil samples were taken from all six native field sites used in the field experiment. These soil samples served as an inoculum for soil-biota treatments to all native and invasive individuals. For this, soil material was sampled about 0.5 m south of the southwestern corner of each experimental plot. After careful sod removal, a volume of 1 l soil was taken per plot, sieved through a 2 mm mesh and collected in a sterilized bucket. Separate soil samples from all plots were pooled and merged by site and served as the site-specific donor substrate. Soil sampling equipment was sterilized between sites to avoid cross-contamination.

All 12 population origins incorporated in the field experiment were also used in the greenhouse with three seed families randomly chosen out of the five used in the field. For each seed family, each one individual was grown with soil addition from

one of the six field sites or only using standard substrate (control). Standard substrate consisted of 60% fine sand provided by the Botanical Garden of Kiel University and 40% unfertilized potting soil (F.E. Typ Nullerde, HAWITA Gruppe GmbH, Vechta, Germany) constituting an environment especially low in nutrients. This led to a total of seven different treatments for each seed family, thus resulting in a total of 252 individuals in the greenhouse experiment. All individuals were transferred to 1.5 l planting pots filled with 1.26 l standard substrate supplemented either by 0.14 l of soil collected from one of the six field sites (9:1 standard substrate:field soil) or an additional 0.14 l standard substrate for the control group. The standard substrate was processed by an autoclave (Webeco Dampf-Sterilisator, Matachana Germany GmbH, Selmsdorf, Germany) to reduce already present soil biota to a minimum. Each pot additionally received 3 g slow-release fertilizer (2.14 g/l) (Basacote Plus 6M 16 + 8 + 12 (+ 2 + 5), Compo Expert GmbH, Münster, Germany) corresponding to low levels of nutrient availability as per the manufacturer's specifications. Planting pots were put on saucers and distributed in the greenhouse. Their position on benches was randomized every week. Predatory mites and sticky traps were installed at the beginning of the experiment to reduce infestation risk with insects. After one month, an insecticide was used on all plants (Spruzit Schädlingsfrei, W. Neudorff GmbH KG, Emmerthal, Germany), and milk and neem oil were applied to all individuals to prevent the spread of mildew. Throughout the experiment all plants were watered with 75 ml of tap water every 1–3 days as needed. Excess water from the saucers was emptied after every watering.

After the experimental runtime, monitoring and biomass harvest were carried out analogous to the field experiment. SLA and LDMC were assessed after 4 weeks and 12 weeks, respectively.

Statistical analysis

Statistical analyses were performed with R (Version 4.1.1) (R Core Team 2019). For the field experiment, a linear mixed effects model was fitted using lme4 (Version 1.1.27) (Bates et al. 2015) and lmerTest (Version 3.1.3) (Kuznetsova et al. 2017). Response variables were transformed if necessary (s. Suppl. material 1: table S1 for transformations used). We included origin (native/invasive) as a fixed effect and the random intercept for plot nested in site and seed family nested in population. We performed a correlation test (function rcorr from the package Hmisc (Harrel 2021), type = "pearson") with the environmental variables. Mean moisture was significantly correlated with maximum plant height, C:N ratio as well as cover of bare soil, whereas relative light was significantly correlated with maximum plant height, α-diversity as well as cover of bare soil, respectively. Soil pH was significantly correlated with α-diversity. Subsequently we excluded mean moisture, pH and relative light intensity as covariates in model fitting. We included number of leaves one week after planting, population density of *J. vulgaris* individuals as well as α-diversity (i.e. number of species), C:N ratio, maximum vegetation height and percentage of bare soil in the monitoring plot as covariates in the full model. The best model was subsequently selected using the step

function (lmerTest) and retained covariates were additionally tested for their interaction with the fixed effect origin in the final model. For survival and herbivory, we fitted generalized linear mixed effects models using the binomial-family and the same structure as for the other variables; however, model selection was done manually.

Similarly, for the greenhouse experiment, we fitted a lmer with origin and provenance of the soil (site) as fixed effects. As a covariate we included either the respective response variables' value at the beginning of the experiment or the initial number of leaves if no starting value was available (for biomass variables, SLA, LDMC). We added the random intercept for seed family nested in the population. For the number of leaves, we fitted a glmer with the poisson family. Differences between the treatments were examined using the Tukey post-hoc test in emmeans (Version 1.7.0) (Lenth 2019). All plots were created using ggplot2 (Version 3.3.5) (Wickham 2016). Predicted values for response variables used in plots were obtained using effects (Version 4.1.4) (Fox and Weisberg 2018, 2019).

Data availability

The datasets generated during and/or analyzed during the current study as well as the code used for analysis are available from the corresponding author upon reasonable request.

Results

Field experiment

After 14 weeks of experimental runtime, individuals originating from the invasive range had developed larger rosettes (Table 1, Suppl. material 1: table S2) and showed a significantly higher aboveground biomass than those from the native range (Fig. 1a). There was no difference in the belowground biomass (Fig. 1b), which led to a smaller root:shoot ratio in invasive origins (Fig. 1c).

Irrespective of origin, C:N ratio and maximum height of the vegetation in the monitoring plot displayed a significantly negative relationship with *J. vulgaris* belowground and total biomass as well as with length of the longest leaf (not shown, Table 1). The higher the maximum vegetation, the higher was also the number of individuals with signs of herbivory (Table 1) and this pattern was more pronounced in native than in invasive individuals (Fig. 1d, Table 1). There was no difference in survival depending on origin (Table 1).

For functional leaf traits, no significant origin effect could be detected (Table 2, Suppl. material 1: table S3). Specific leaf area (SLA) after 6 weeks of experimental runtime, however, was negatively correlated with the number of species in the monitoring plot (α-diversity) for individuals originating from the species' invasive range (Fig. 2a). After 14 weeks, SLA was higher with increasing height of the surrounding vegetation, irrespective of plant origin (Fig. 2b). In addition, after 14 weeks, there was an interaction effect of LDMC with increasing α-diversity displaying an increase in LDMC in invasive individuals but no such pattern in native origins (Fig. 2c).

Table 1. Field experiment – performance traits. Results from the ANOVA for the linear-mixed effects and generalized-mixed effects model (Herbivory and Survival) in the field experiment for performance traits. Significant effects ($p<0.05$) are printed in bold.

	Rosette Expansion [cm²]						Number of Leaves [count]					
	NumDf	DenDF	F	P	NAT	INV	NumDf	DenDF	F	P	NAT	INV
Origin	1	287.15	7.1117	**0.008**	147.09 ± 216.97	194.14 ± 251.87	1	9.602	4.6268	0.058	7.29 ± 5.82	8.63 ± 6.76
Week 1**	1	297.41	5.1658	**0.024**			1	227.745	22.79	**<0.001**		
C:N ratio	NA	NA	NA	NA			NA	NA	NA	NA		
Max. vegetation height	NA	NA	NA	NA			NA	NA	NA	NA		
Origin × C:N ratio	NA	NA	NA	NA			NA	NA	NA	NA		
Origin × Max. vegetation height	NA	NA	NA	NA			NA	NA	NA	NA		
	Length of longest Leaf [cm]						**Aboveground Biomass [g]**					
	NumDf	**DenDF**	**F**	**P**	**NAT**	**INV**	**NumDf**	**DenDF**	**F**	**P**	**NAT**	**INV**
Origin	1	286.431	0.5499	0.458	12.07 ± 6.48	13.94 ± 8.23	1	290.39	7.6368	**0.006**	0.60 ± 1.95	1.01 ± 2.82
Week 1**	1	298.693	10.7502	**0.001**			1	303.44	10.4424	**0.001**		
C:N ratio	1	7.334	6.8443	**0.033**			NA	NA	NA	NA		
Max. vegetation height	1	16.219	5.289	**0.035**			NA	NA	NA	NA		
Origin × C:N ratio	1	285.911	0.0208	0.885			NA	NA	NA	NA		
Origin × Max. vegetation height	1	286.344	0.3022	0.583			NA	NA	NA	NA		
	Belowground Biomass [g]						**Total Biomass [g]**					
	NumDf	**DenDF**	**F**	**P**	**NAT**	**INV**	**NumDf**	**DenDF**	**F**	**P**	**NAT**	**INV**
Origin	1	281.277	0.2909	0.590	0.51 ± 0.57	0.53 ± 0.52	1	290.009	0.0228	0.880	1.11 ± 2.47	1.54 ± 3.31
Number of leaves	1	315.251	26.8191	**<0.001**			1	289.342	18.0332	**<0.001**		
C:N ratio	1	27.973	5.6967	**0.024**			1	29.04	4.3788	**0.045**		
Max. vegetation height	1	29.692	4.8105	**0.036**			1	30.241	5.9063	**0.021**		
Origin × C:N ratio	1	278.043	0.7901	0.374			1	278.227	0.1853	0.667		
Origin × Max. vegetation height	1	279.297	0.0001	0.993			1	279.264	0.0392	0.843		
	Root:Shoot Ratio											
	NumDf	**DenDF**	**F**	**P**	**NAT**	**INV**						
Origin	1	54.908	11.7481	**0.001**	2.31 ± 2.27	1.76 ± 1.70						
Number of leaves	1	290.887	0.4528	0.502								
J. vulgaris density	NA	NA	NA	NA								
Max. vegetation height	NA	NA	NA	NA								
Origin × *J. vulgaris* density	NA	NA	NA	NA								
Origin × Max. vegetation height	NA	NA	NA	NA								
	Herbivory [probability]						**Survival [probability]**					
	Estimate		**Z**	**P**	**NAT**	**INV**	**Estimate**		**z**	**P**	**NAT**	**INV**
Origin	14.4039		2.317	**0.021**	0.13 ± 0.34	0.11 ± 0.32	0.1614		0.403	0.687	0.86 ± 0.35	0.84 ± 0.36
Number of leaves	NA		NA	NA			NA		NA	NA		
J. vulgaris density	-0.0381		-1.487	0.137			NA		NA	NA		
Max. vegetation height	0.1737		2.821	**0.005**			NA		NA	NA		
Origin × *J. vulgaris* density	-0.0382		-1.013	0.311			NA		NA	NA		
Origin × Max. vegetation height	-0.1296		-2.27	**0.023**			NA		NA	NA		

J. vulgaris density = density of naturally occurring individuals in experimental plot; Number of Leaves was counted at initial monitoring one week after planting; †Week 1 refers to the values of the response variable at the start of the experiment, e.g. for Rosette Expansion (week 14) this is the Rosette Expansion at week 1. NAT = mean and standard deviation for native individuals. INV = mean and standard deviation for invasive individuals.

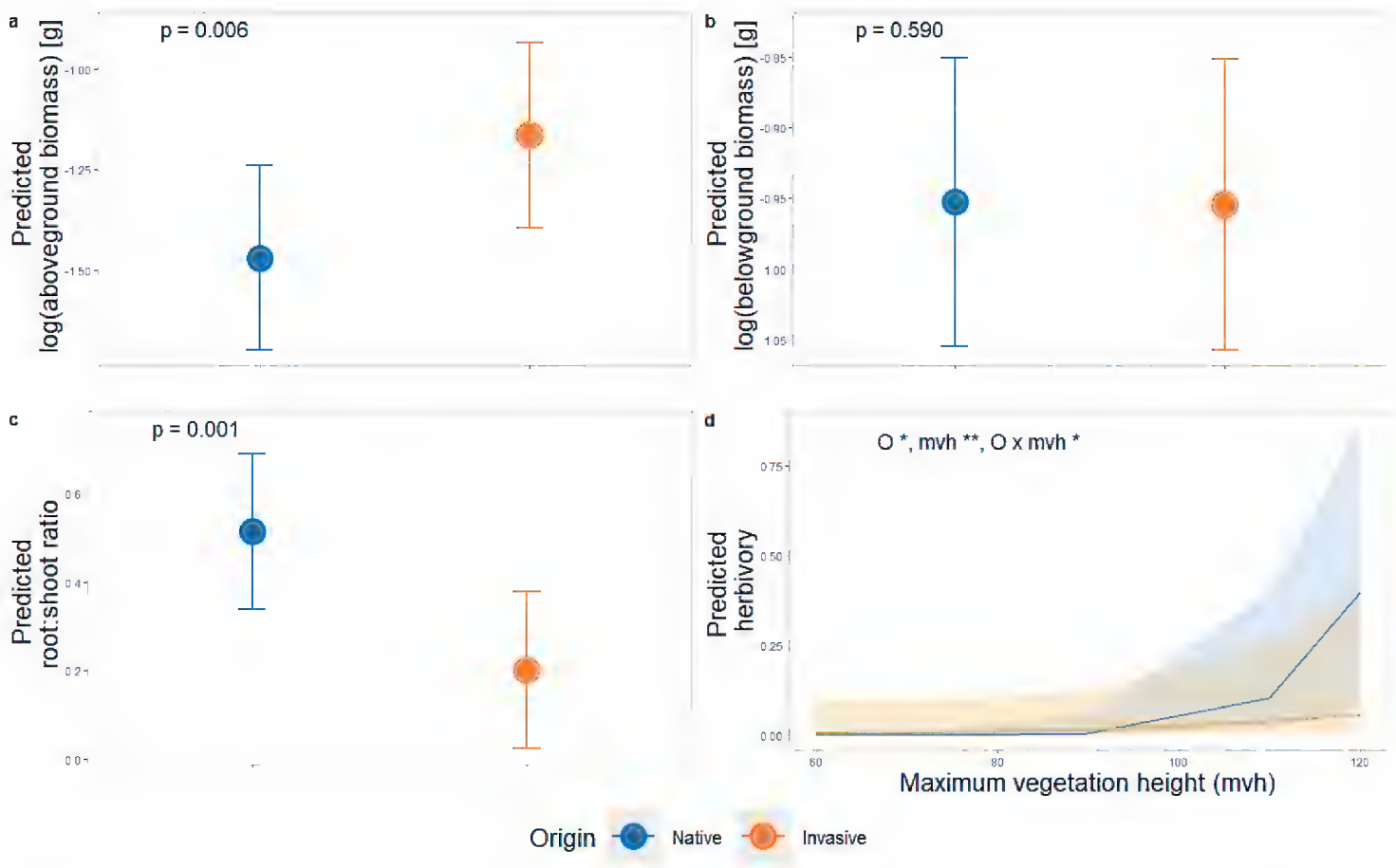

Figure 1. Origin effects (field experiment). Response of performance (**a–c**) traits in relation to origin of the seeds for each individual. Data shown are predicted values from the model ± SE. Native individuals (left, blue) originated from the field sites where the experimental plots were located. Invasive individuals (right, orange) originate from the Pacific Northwest. Herbivory (**d**) was assessed as a binary trait (presence/absence) only. N = 319 (**a–c**) and n = 322 (**d**). For depiction of raw data s. Suppl. material 1: fig. S3.

Table 2. Field experiment – functional traits. Results from the ANOVA for the linear-mixed effects in the field experiment for functional leaf traits. Significant effects ($p<0.05$) are printed in bold.

	SLA (week 6)						LDMC (week 6)					
	NumDf	**DenDF**	**F**	**P**	**NAT**	**INV**	**NumDf**	**DenDF**	**F**	**P**	**NAT**	**INV**
Origin	1	156.816	1.6254	0.204	21.84 ± 6.16	20.37 ± 4.17	1	43.488	3.1219	0.084	0.13 ± 0.03	0.13 ± 0.02
Number of leaves	1	173.993	3.6489	0.058			1	170.423	0.8594	0.355		
α-Diversity	1	7.592	12.0547	**0.009**			NA	NA	NA	NA		
C:N ratio	1	5.373	5.8519	0.056			NA	NA	NA	NA		
Origin × α-Diversity	1	139.819	6.3232	**0.013**			NA	NA	NA	NA		
Origin × C:N ratio	1	155.856	0.4553	0.500			NA	NA	NA	NA		
	SLA (week 14)						**LDMC (week 14)**					
	NumDf	**DenDF**	**F**	**P**	**NAT**	**INV**	**NumDf**	**DenDF**	**F**	**P**	**NAT**	**INV**
Origin	1	284.181	1.4873	0.224	27.38 ± 7.54	27.29 ± 7.49	1	292.377	0.1939	0.660	0.11 ± 0.02	0.09 ± 0.02
Number of leaves	1	299.233	1.469	0.226			1	255.374	0.7518	0.387		
Max. vegetation height	1	31.503	5.1708	**0.029**			NA	NA	NA	NA		
Origin * Max. vegetation height	1	276.967	1.435	0.232			NA	NA	NA	NA		
α-Diversity	NA	NA	NA	NA			1	27.654	2.552	0.122		
C:N ratio	NA	NA	NA	NA			1	16.52	3.7026	0.072		
Origin × α-Diversity	NA	NA	NA	NA			1	276.883	6.7717	**0.010**		
Origin × C:N ratio	NA	NA	NA	NA			1	280.836	0.0623	0.803		

Number of Leaves was counted at initial monitoring one week after planting; SLA = specific leaf area, LDMC = leaf dry matter content.

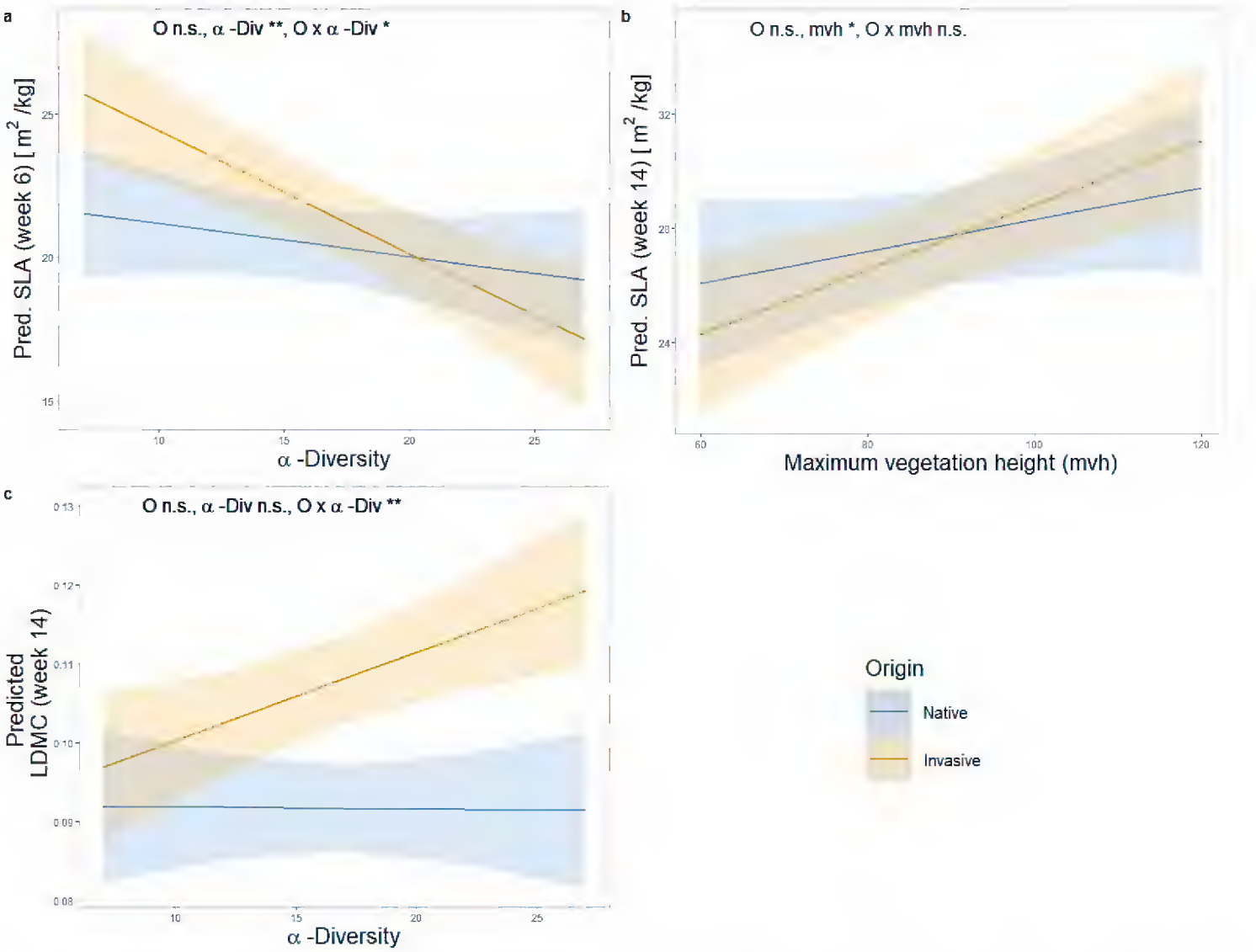
a
O n.s., α -Div **, O x α -Div *
Pred. SLA (week 6) [m2 /kg]
α -Diversity
b
O n.s., mvh *, O x mvh n.s.
Pred. SLA (week 14) [m2 /kg]
Maximum vegetation height (mvh)
c
O n.s., α -Div n.s., O x α -Div **
Predicted LDMC (week 14)
α -Diversity
Origin
Native
Invasive

Figure 2. Origin effects × covariate (field experiment). Effects of origin in interaction with α-diversity (**a, c**) and maximum vegetation height of surrounding vegetation within the experimental plot (**b**). Data shown are predicted values from the model with upper and lower range. O = origin, α-Div = α-diversity, mvh = maximum vegetation height (of surrounding vegetation), SLA = specific leaf area, LDMC = leaf dry matter content. Week 6 and Week 14 indicates that the leaves for analysis were harvested after 6 weeks of experimental runtime or at the final harvest of the plants after the entire experimental runtime, respectively. N = 193 (**a**), 311 (**b**), 319 (**c**). SLA after 6 weeks was only taken for plants that had a sufficient number of healthy leaves and therefore constitutes a reduced subset. For depiction of raw data s. Suppl. material 1: fig. S4.

Greenhouse experiment

In the greenhouse experiment, there was no difference in biomass depending on the origin of the individuals (Table 3, Suppl. material 1: table S4). Provenance of the soil (treatment) did not affect the aboveground biomass (Fig. 3a) and root:shoot ratio (Fig. 3d) but belowground biomass (Fig. 3b) and total biomass differed significantly between the treatments (Fig. 3c). Number of leaves was the only trait exhibiting significant soil provenance × population origin interaction effects, but post-hoc test revealed no significant difference for origins within any given site.

For the functional traits SLA and LDMC, no difference depending on the origin of the individuals could be detected (Table 4, Suppl. material 1: table S5). However, soil provenance incurred differences in SLA after four (Fig. 4a) and 12 weeks

Table 3. Greenhouse experiment – performance traits. Results from the ANOVA for the linear-mixed effects in the greenhouse experiment for performance traits. Significant effects ($p<0.05$) are printed in bold. Treatment refers to the provenance of the added soil. All soils originate from field sites within the species' native range.

	Rosette Expansion [cm²]						Number of Leaves				
	NumDf	DenDF	F	P	NAT	INV	Chisq	Df	Pr	NAT	INV
Origin	1	10.302	0.3555	0.563	515.6 ± 198.34	525.75 ± 185.82	0.343	1	0.558	26.35 ± 8.19	25.19 ± 8.42
Treatment	6	224.597	2.6195	**<0.001**			19.756	6	**0.003**		
Initialǂ	1	224.9	3.93	0.090			19.2468	1	**<0.001**		
Origin × Treatment	6	224.529	0.9115	0.487			24.9001	6	**<0.001**		

	Length of longest Leaf [cm]					
	NumDf	DenDF	F	P	NAT	INV
Origin	1	10.007	3.462	0.092	17.83 ± 3.80	18.66 ± 3.83
Treatment	6	200.665	3.9741	**<0.001**		
Initialǂ	1	220.839	16.663	**<0.001**		
Origin × Treatment	6	200.924	1.3928	0.219		

	Aboveground Biomass [g]						Belowground Biomass [g]					
	NumDf	DenDF	F	P	NAT	INV	NumDf	DenDF	F	P	NAT	INV
Origin	1	10.211	2.915	0.160	4.80 ± 2.15	5.39 ± 2.66	1	223	0.0646	0.800	8.77 ± 5.39	2.66 ± 8.77
Treatment	6	225.441	2.0788	0.057			6	223	3.7241	**0.002**		
Number of leaves	1	224.85	2.4574	0.118			1	223	0.0208	0.886		
Origin × Treatment	6	225.216	1.1429	0.338			6	223	0.4702	0.930		

	Total Biomass [g]						Root:Shoot ratio					
	NumDf	DenDF	F	P	NAT	INV	NumDf	DenDF	F	P	NAT	INV
Origin	1	10.65	1.8419	0.203	12.24 ± 8.20	14.24 ± 8.78	1	36.516	0.3564	0.554	1.77 ± 1.25	1.65 ± 1.26
Treatment	6	226.95	3.7727	**0.001**			6	187.414	2.0053	0.067		
Number of leaves	1	171.56	0.1229	0.726			1	190.777	0.0396	0.842		
Origin × Treatment	6	226.55	0.9688	0.447			6	186.814	0.2409	0.962		

Number of leaves was counted at initial monitoring. Initialǂ refers to the values of the response variable at the initial monitoring, e.g. for Rosette Expansion (week 12) this is the Rosette Expansion at the initial monitoring, Treatment refers to the provenance of the soil used.

Table 4. Greenhouse experiment – functional traits. Results from the ANOVA for the linear-mixed effects in the field experiment for functional leaf traits. Significant effects ($p<0.05$) are printed in bold.

	SLA (week 4)						LDMC (week 4)					
	NumDf	DenDF	F	P	NAT	INV	NumDf	DenDF	F	P	NAT	INV
Origin	1	10.142	0.9933	0.342	23.99 ± 4.46	22.73 ± 3.55	1	9.911	0.1945	0.669	0.12 ± 0.00	0.12 ± 0.02
Treatment	6	202.852	2.807	**0.012**			6	203.173	3.3796	**0.003**		
Number of leaves	1	235.607	3.1885	0.075			1	205.374	10.3484	**0.002**		
Origin × Treatment	6	202.57	0.4798	0.823			6	202.779	1.0921	0.368		

	SLA (week 12)						LDMC (week 12)					
	NumDf	DenDF	F	P	NAT	INV	NumDf	DenDF	F	P	NAT	INV
Origin	1	10.214	1.6375	0.229	21.22 ± 3.33	19.95 ± 3.35	1	9.894	0.0999	0.759	0.20 ± 0.03	0.20 ± 0.04
Treatment	6	200.084	3.7331	**0.002**			6	200.154	1.2052	0.305		
Number of leaves	1	232.749	8.0692	**0.005**			1	219.386	1.3717	0.243		
Origin × Treatment	6	199.909	0.2384	0.963			6	199.852	0.177	0.983		

SLA = Specific leaf area, LDMC = leaf dry matter content.

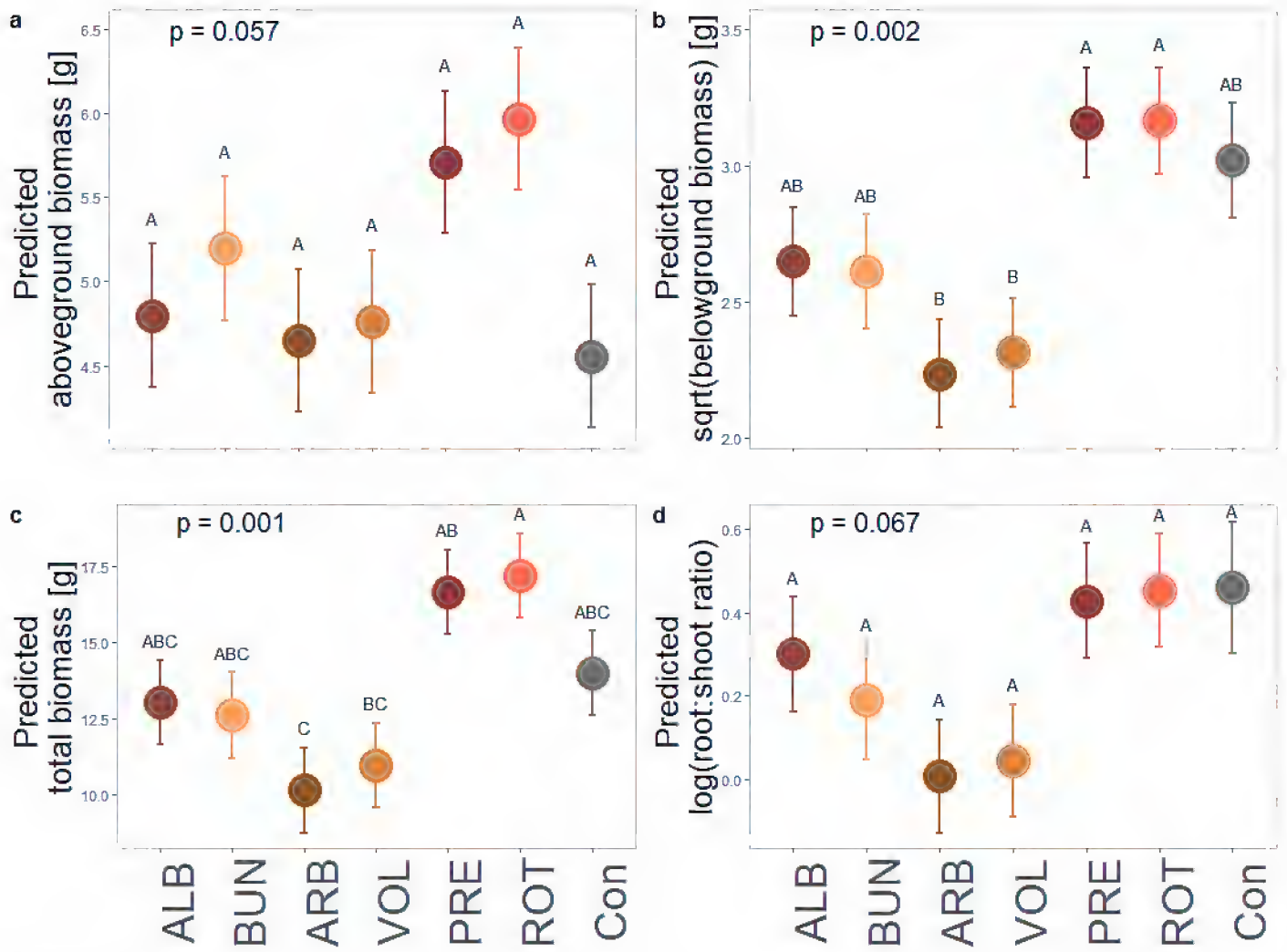

Figure 3. Treatment effects on performance traits (greenhouse experiment). Effects of soil provenance in the greenhouse experiment. Data shown are predicted values from the model ± SE. Different colors represent different soil origins (only soil from native sites were included in this experiment). Different letter combinations in the panels indicate significant differences according to the Tukey post-hoc test. ALB = Albersdorf, ARB = Arpsdorf, BUN = Bünsdorf/Wittensee, Con = Control (no soil added from any field site), PRE = Preetz, ROT = Rotenhahn/Eidertal, VOL = Vollstedter See. For location information see Suppl. material 1: fig. S1. N(**a**) = 250, n(**b**) = 238, n(**c**) = 251, n(**d**) = 230. For depiction of raw data s. Suppl. material 1: fig. S5.

(Fig. 4b), and LDMC differed significantly depending on soil provenance after four weeks (Fig. 4c). No differences in LDMC were observed after 12 weeks of experimental runtime (Fig. 4d).

Discussion

Since its initial appearance in the Pacific Northwest about a century ago, there was, theoretically, ample time for adaptive evolutionary adjustment to occur in *Jacobaea vulgaris* populations. Local adaptation is supposed to lead to fitness advantages of invasive populations adjusted to environmental conditions in the novel range, including an absence of specialist herbivores (Kawecki and Ebert 2004). However, it would be expected that such a shift would not pay off anymore when back-introduced to the species' native range (Eurasia) and rather provide evidence of maladaptation. Contrary to this gen-

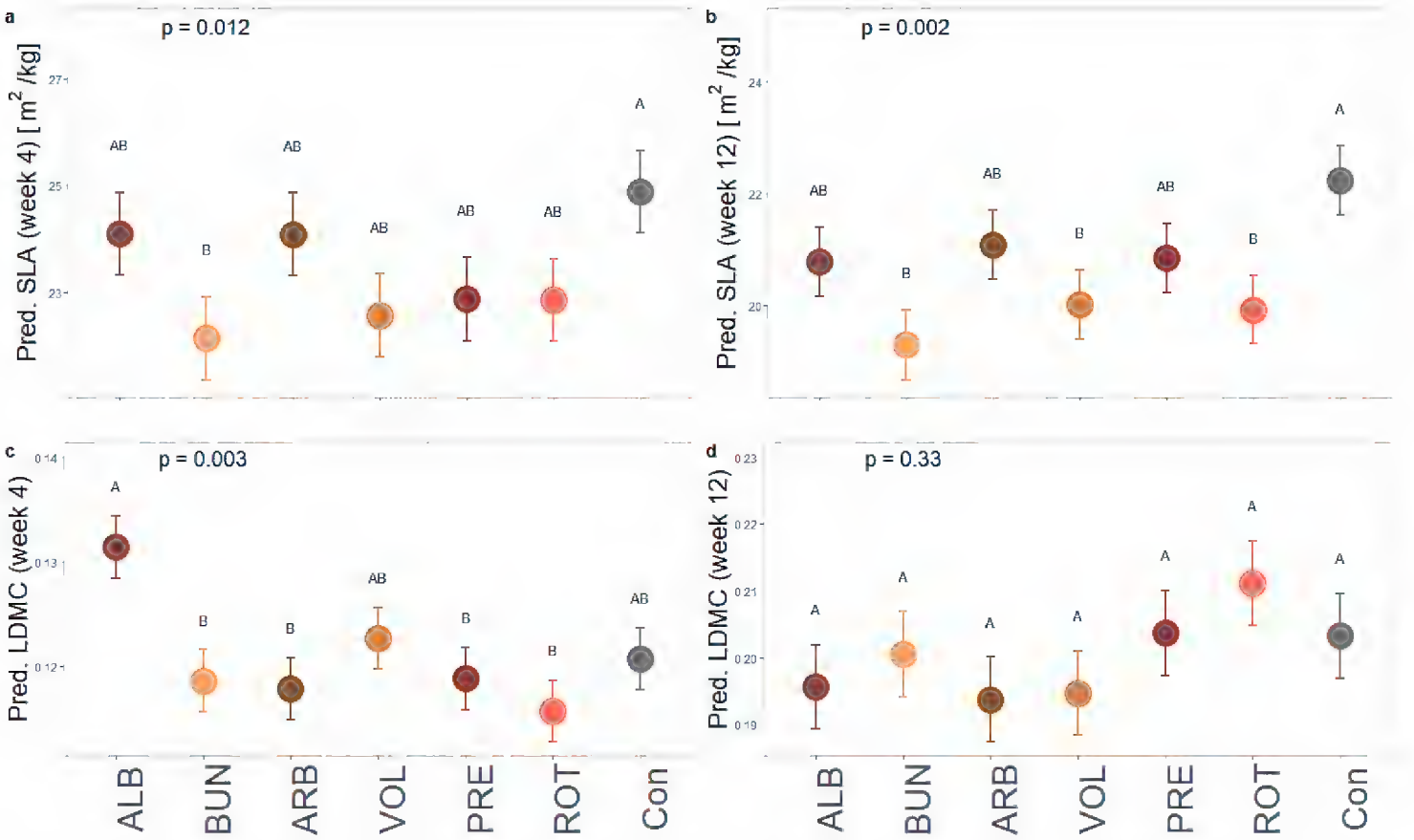

Figure 4. Treatment effects on functional traits (greenhouse experiment). Effects of soil provenance in the greenhouse experiment. Data shown are predicted values from the model ± SE. Different colors represent different soil origins (only soil from native sites were included in this experiment). Different letter combinations in the panels indicate significant differences according to the Tukey post-hoc test. ALB = Albersdorf, ARB = Arpsdorf, BUN = Bünsdorf/Wittensee, Con = Control (no soil added from any field site), PRE = Preetz, ROT = Rotenhahn/Eidertal, VOL = Vollstedter See. For location information see Suppl. material 1: fig. S1. N(**a**) = 215, n(**b**) = 248, n(**c**) = 251, n(**d**) = 249. For depiction of raw data s. Suppl. material 1: fig. S6.

eral assumption, in the present study, invasive origins outperformed the native origins when (re-)transplanted to native field sites in Northern Germany. Our findings are, in fact, more in line with considerations associated with the potential risk of cryptic invasions triggered by back-introductions of invasive genotypes and multiple factors might have contributed to our observation (hypothesis I).

Origin effects and maladaptation

There is some evidence that specialist herbivores prefer invasive individuals of *J. vulgaris* over native ones (Lin et al. 2015). In the experimental area of Northern Germany, these specialist herbivores are naturally present. However, the specialist *Tyria jacobaeae* usually prefers larger individuals (van der Meijden 1976) while additionally, theory and evidence suggest that generalist herbivores prefer native origins (Keane 2002; Joshi and Vrieling 2005). The fact that our transplants were relatively unattractive to specialist herbivores while previous studies predict higher attractiveness of native origins to generalists, might have contributed to the observed increased performance in invasive origins and increased occurrence of herbivory in native origins. For moths and

butterflies, specialist species were found to prefer lower vegetation compared to generalists (Pöyry et al. 2006), which in combination with the significant herbivory × maximum vegetation height interaction in our experiment, further corroborates this assumption.

In contrast, the absence of any origin-dependent differences in the greenhouse experiment was unexpected given previous studies with *J. vulgaris* showing higher performance of invasive origins (Joshi and Vrieling 2005). Different factors could explain this outcome. First of all, greenhouse experiments, by definition, involve herbivory to be kept at a minimum. This design therefore neither favors native (more specialists) nor invasive (more generalists) individuals of *J. vulgaris* in a greenhouse. Secondly, the greenhouse experiment was set up later in the year while relying on the same growing material. Accordingly, the experimental individuals for the greenhouse experiment were older than the transplants. Seasonal timing might thus have additionally affected plant development differently.

In the field experiment, the invasive individuals might also have benefitted from atypically high temperature and decreased precipitation during the experimental runtime (Broennimann et al. 2007; Early and Sax 2014). During the summer of 2019, the average temperature in Germany was 2.9 °C higher and precipitation on average was 27.7% lower than predicted according to the international climatological reference period (Deutscher Wetterdienst 2020). For the populations included in this experiment, the invasive range is both warmer (native: 15.6 ± 1.38 C; invasive: 16.21 ± 1.18 °C) and drier (native: 232.5 ± 6.75 mm; invasive: 125.5 ± 34.49 mm) during the warmest quarter on average (Data from BioClim, accessed Nov. 10th 2020; Fick and Hijmans 2017), so the present finding might be indicative of a possible climatic niche shift in invasive origins (Broennimann et al. 2007). However, previous studies with *J. vulgaris* showed that, inter alia, competitive ability and regrowth (Lin et al. 2015), growth and regrowth (Lin et al. 2018) as well as growth, photosynthetic rate, and LMR (Lin et al. 2019) differ between native and invasive origins of *J. vulgaris*, but these differences were explicitly not driven by climatic conditions.

The role of environmental conditions and soil-borne effects

In the present study, the provenance of soil (treatment) differently impacted *J. vulgaris* performance (e.g., aboveground biomass), thereby confirming that soil-borne biotic effects contribute to differentiation among populations, as expected (hypothesis III). Strong negative feedbacks on *J. vulgaris* populations themselves have previously been shown in native populations (van de Voorde et al. 2011, 2012a). They furthermore increased with population density (van de Voorde et al. 2012a) and over time in an interspecific competition setting (Bezemer et al. 2018). Additionally, other species were found to exert PSFs on *J. vulgaris* (Bezemer et al. 2006; van de Voorde et al. 2011; Wubs and Bezemer 2018), showing that PSFs are a factor not to be neglected when studying this species' performance and population dynamics.

Knowledge about soil provenance × plant origin interactions in general is lacking for this model species to date and we found no signs for enemy release on the belowground level as shown for *Centaurea maculosa* performance (Callaway et al. 2004). Our findings are more in line with a study on *Verbascum thapsus* that found signs of

coevolution between plants and soil microbes on the between-population level but not between ranges of origin (Dieskau et al. 2020). To ensure that the patterns observed in our experiment are not co-affected by differences in soil properties, soil washes as applied by Dieskau et al. (Dieskau et al. 2020) should preferably be used in future experiments to address pure biotic effects most precisely.

In the present experiment, maximum vegetation height (strongly linked to light availability with $r = -0.62$, $p<0.001$ with Pearson's rank) was a relevant environmental factor for both origins, with the typical responses of increasing specific leaf area with decreasing light availability (Cornelissen 1992). LDMC varied more in the further course of the experiment, whereas variation in SLA was higher earlier in the experiment with different responses to increasing α-diversity depending on the range origin of the transplants. Given that the invasive individuals allocated more biomass by the end of the experiment, this pattern points towards a reaction to different environmental conditions rather than a sign of stress. Higher phenotypic variation was not only shown to pay off for invasive species compared to native congeners (Funk 2008), but may also apply within a species when comparing native and invasive origins (Caño et al. 2008; Hock et al. 2019). Under these considerations, our results suggest that high phenotypic plasticity might be one important factor contributing to the invasion success of *J. vulgaris* as well.

In summary, we cannot conclude explicitly which factors are the main drivers of increased performance of invasive transplants in the species' native range (hypothesis II). It is, therefore, also difficult to accurately predict the long-term consequences of back-introduction of propagules or individuals of invasive origin into the species' native range. However, genetic admixture might accelerate geographic expansion and invasion (Qiao et al. 2019), thus re-introduction of these invasive genotypes could therefore be problematic. Re-introduction might return originally common but then modified ("adapted") genotypes that have undergone selection in the invasive range. At the same time, it could also add genotypes from other parts of the species' native range, especially in *J. vulgaris*. In our experiment, we cannot determine whether the invasive transplants are re-introduced in the strict sense or originally came from other parts of the species' native range, especially as invasive populations of *J. vulgaris* were found to probably be admixed before spreading within the invasive range (Doorduin 2012). In Northern Germany, *J. vulgaris* is assumed to form large panmictic metapopulations (Jung et al. 2020). However, for other species, intraspecific hybridization was previously shown to promote invasion processes (Kolbe et al. 2004; Geiger et al. 2011) and these findings could also apply to cryptic invasions. Therefore, introducing genetic material from the invasive range irrespective of its history, may evoke concerns among nature conservationists for the species' native range.

Conclusion

Invasive genotypes of *J. vulgaris* seem to exhibit higher levels of phenotypic variation, giving them more leeway when confronted with changing environmental conditions. This appears to be especially applicable under favorable environmental conditions as

found in the field experiment, but our findings do not preclude that invasive genotypes might also show superior performance under certain more stressful conditions. It is probable that invasive genotypes, in the future, might do even better in the species' native range, as the environmental conditions might converge to the environmental conditions of the invasive regions.

With regard to a possible cryptic invasion of *J. vulgaris* in the native range, the present study suggests two main messages: Primarily, (back-) introduction of propagules from the invasive ranges of *J. vulgaris* should be prevented as much as possible. Secondly, it might be beneficial to invest more in further identifying the characteristics that decrease the susceptibility of a field site for *J. vulgaris* in general. For *J. vulgaris*, in particular, highly controlled greenhouse experiments under realistic conditions should aim to validate the observed patterns in generative (second-year) flowering plants and assess fitness traits.

However, it is likely that cryptic invasions will occur more often than identified so far. To date, invasion research mostly focuses on the unidirectional introduction into the novel range, and little is known about the possibility of back-introduction. Furthermore, knowledge about the frequency with which back-introductions happen is so far lacking. Generally, pathways of biological invasions are complex and vary in their relative importance over time (Hulme 2009; Essl et al. 2015); climate change may further increase human movement and subsequently the spread of non-native biota (Robinson et al. 2020). Future approaches elucidating the risk of cryptic invasions should apply more controlled back-introduction experiments as real-world tests with further candidate species that have shown to be successful invaders in the past.

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Supplementary material 1

Supplementary information

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Data type: images, tables (word document)

Explanation note: Population information. Schematic overview of one experimental plot with planting scheme. Transformations of variables. Mean values for performance traits (field experiment). Mean values for functional leaf traits (field experiment). Mean values for performance traits (greenhouse experiment). Mean values for functional leaf traits (greenhouse experiment). Origin effects (field experiment). Origin effects × covariate (field experiment). Treatment effects on performance traits (greenhouse experiment). Treatment effects on functional traits (greenhouse experiment).

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